

Wildfire effects on plant species richness at multiple spatial scales in forest communities of the southern Appalachians

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Summary

1 We fitted species-area curves to the power function and examined changes in the parameters to quantify changes in species richness of all plants together, trees only and non-trees over five scales of magnitude (0.01 m² to 400 m²) after a wildfire in the Linville Gorge Wilderness Area, North Carolina, USA.

2 Increases in species richness of all plants together occurred after the fire at all scales and increased in magnitude as scale increased. However, a lack of change in the slopes (z-values) of species-area curves indicates that proportional changes were independent of scale of observation below 400 m². Changes in species richness were predominantly driven by immigration, which was significantly related to fire severity. Survival of species present pre-fire was greater than local extinction, but neither was related to severity.

3 Species richness of trees increased at all scales but proportional increases were smaller at larger scales and slopes of species-area curves decreased after the fire. Local seedling recruitment increased species richness at small scales, but low rates of immigration due to dispersal limitation in most species limited increases at larger scales.

4 Directional changes in species richness of non-trees were not always consistent at fine scales but both absolute and relative changes were positive at scales ≥ 1 m² and increased with increasing scale. Slopes of species-area curves increased post-fire because localized patterns of immigration within plots resulted in little mixing of species at small scales but large changes in species richness at larger scales.

5 Fire in the southern Appalachians increases plant species richness within local communities, but rates of species turnover and patterns of beta diversity are maintained by local recruitment of tree seedlings at small scales and immigration of herb, shrub and vine species at larger scales.

6 Although decreased levels of competition after disturbance promote species coexistence at small scales, changes in species richness at larger scales are determined by the degree that the local community is linked to the species pool of the surrounding landscape through processes related to dispersal, particularly mass effects.

Key-words: disturbance, fire, Linville Gorge Wilderness, immigration, mass effects, pine-oak forests, scale, southern Appalachians, species-area curves

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Introduction

Although the role of disturbance in structuring natural communities has received much attention (Loucks 1970; Sousa 1984; Pickett & White 1985), most insight into its effects on diversity have come from observations

at single, relatively small spatial scales (≤ 10 m²). Previous work suggests that disturbance promotes the coexistence of species at small scales by reducing the dominance of strong competitors and allowing the establishment of less competitive species, thereby increasing overall richness (Huston 1979; Denslow 1985). Although field studies of community response to natural disturbance generally support this prediction (e.g. Platt 1975; Connell 1978; Denslow 1980),

few have examined whether results are consistent at larger scales. Those incorporating observations at multiple scales have shown that resulting patterns of diversity are frequently scale dependent, but have only compared post-disturbance data among communities disturbed at different frequencies (Schwilk *et al.* 1997; Glitzenstein *et al.* 2003; Keeley & Fotheringham 2003; Weiher & Howe 2003; Uys *et al.* 2004). In order to examine the role of processes such as immigration, extinction and survivorship that drive changes in species richness at the local community level (MacArthur & Wilson 1967; Brown & Peet 2003) a comparison of pre- and post-disturbance communities is necessary.

A multiscale approach provides insight into patterns observed at one scale, but created by processes occurring at other scales (Levin 1992). Schmid & Wilson (1985) provided one of the earliest conceptual models of how different processes determine species richness in plant communities at different spatial scales. At small scales ($< 1 \text{ m}^2$), competition and niche relations are major determinants of species richness. Provided that a more or less homogeneous environment exists within an area, the importance of niche relations should not vary through space. At intermediate scales ($1\text{--}100 \text{ m}^2$) spatial heterogeneity is created by the presence of various microsites, allowing for coexistence of species differing in resource requirements or competitive abilities. This turnover, or differentiation diversity, is referred to by Schmid & Wilson as beta diversity following Whittaker (1960). Beta diversity will increase as competitive exclusion at small scales restricts species to sites where they are best suited. At larger scales ($> 100 \text{ m}^2$), species richness is determined by mass effects (Schmid & Whittaker 1981). Mass effects occur when high propagule pressure from favourable source habitats results in the occurrence of species in sink habitats where they are unable to persist in the absence of immigration. The scale at which mass effects occur is determined by the dispersal abilities of species present in surrounding communities and the spatial distribution of species in relation to environmental heterogeneity across a landscape.

Multiple processes occurring simultaneously at different scales may result in scale-dependent patterns of change in species richness after disturbance. The magnitude and even direction of change may vary depending on the relative influences of the processes involved. At small scales ($< 1 \text{ m}^2$) disturbance weakens the intensity of competition, and thus the importance of niche relationships. Platt (1975) found that localized disturbances (approximately $0.2\text{--}0.3 \text{ m}^2$) created by digging badgers reduced direct competition and enabled coexistence in a guild of fugitive prairie plant species. At intermediate spatial scales ($1\text{--}100 \text{ m}^2$), species coexistence is promoted by habitat heterogeneity and the resulting pattern of beta diversity. Denslow (1980) suggested that heterogeneous light resources in tropical forest gaps are partitioned among different species depending on their requirements for light. The relative

importance of habitat heterogeneity after disturbance depends on the spatial pattern of the disturbance and the resulting changes in the physical environment. At scales where mass effects may be occurring ($> 100 \text{ m}^2$) the effects of disturbance on net changes in species richness will be dictated by rates of local extinction within the local community and immigration of new species from the surrounding landscape. Mass effects are likely to be important if there are many species in the surrounding landscape capable of dispersing large distances.

The use of species-area curves to assess the impacts of disturbance has proved to be a novel application of one of ecology's longest recognized patterns (Rosenzweig 1995) and has altered the interpretation of the role of disturbance in the maintenance of species diversity (Denslow 1995; Busing & White 1997; Hubbell *et al.* 1999). Species-area curves allow not only a comparison of species richness at multiple spatial scales before and after a disturbance, but also an assessment of change in the rate at which species richness increases with area. Although changes in species richness at a single scale have preoccupied past studies of disturbance, the slope of the species-area relationship is important in determining species richness at larger scales. The most widely accepted equation used to fit species-area curves is the Arrhenius power function

$$S = cA^z$$

where S = the number of species, A = area, and the two fitted parameters c and z are constants where c = species richness at one unit of area (α diversity) and z = the rate at which the number of species increases with area (β diversity) (Rosenzweig 1995; Hubbell 2001; Scheiner 2003). Assuming that disturbance will increase c (richness at small scales), there are three possible outcomes of changes in species richness at larger scales. If z increases, changes in richness will be positive at all scales, but the magnitude of increase will be greater at larger scales. If z decreases and a large enough range of scales has been sampled, then the change in richness will be zero at some intermediate scale and negative at large scales. If z remains the same, then increases will be proportional across scales. Thus, an interpretation of how both c and z change after a disturbance will allow the prediction of both the direction and magnitude of change in species richness, revealing insights into how processes occurring at different scales are affected by disturbance.

The objective of this study was to use species-area curves to determine if changes in plant species richness are consistent across scales after fire in southern Appalachian forests, and to infer how processes occurring at different spatial scales are affected by disturbance. The flora of the southern Appalachians has long drawn the attention of botanists and ecologists (Whittaker 1956; Bartram 1792; Runkle 1981). In the xeric pine and oak forests that cover the mid-elevation slopes and ridges of

this region, fire has historically been the dominant disturbance, recurring every 10–12 years during the 1800s (Barden & Woods 1973; Harmon 1984). Since the late 1930s most wildfires have been suppressed. Previous studies of the effects of fire on species richness have documented increases at single scales (Arthur *et al.* 1998; Elliott *et al.* 1999), but the roles of community level processes such as immigration and local extinction that are potentially driving observed patterns are largely unknown. One of the largest wildfires the region has experienced in the last 50 years recently occurred in the Linville Gorge Wilderness Area, located in western North Carolina, USA. The existence of a network of permanent plots with a nested sampling scheme ranging from 0.01 m² to 400 m² (Newell & Peet 1998) presents a unique opportunity to examine the role of natural disturbance in changes in species richness across five scales of magnitude.

We address three questions. First, are changes in species richness after fire at small scales consistent with those at larger scales? Increases in species richness at small scales may occur from recruitment of species present in the local community, but increases in richness at larger scales will depend on immigration of species from outside the local community. Secondly, what is the effect of fire severity on immigration, survival and extinction in local communities? The relative importance of these processes across varying levels of disturbance severity will be determined by the number of species in the landscape with high potential for dispersal and the degree of resilience exhibited by species in the pre-disturbance community. Thirdly, how do the results of the first two questions change when species are split into different functional groups? Trees, shrubs, vines and herbs differ in terms of their longevity, size and, in particular, their capacity for dispersal. Differences in these life-history attributes are likely to result in different post-fire patterns of species richness from those in all plants taken together.

Methods

STUDY SITE

Linville Gorge is a 4390-ha federally designated wilderness area located in the Pisgah National Forest, Burke County, North Carolina, USA. Elevation ranges from 820 m at the bottom of the gorge to 1250 m on upper ridges. Upper and lower slopes are separated by prominent bluffs that bisect both sides of the gorge. As a result of downcutting from the Linville River, several types of parent material have been exposed. The plots chosen for this study were restricted to upper slopes occurring on the lower quartzite formation, extending from the bluffs to the ridge, where soils are generally thin and coarse, consisting primarily of Typic or Lithic Dystrichepts. Annual precipitation ranges from 1250 to 1625 mm and is highest in the summer months, occurring mostly as rain.

Because of the steep slopes and inaccessibility of the gorge, the vast majority of the landscape is old growth and thought to be representative of pre-settlement forests (Davis 1996). Ridges and bluffs are dominated by *Pinus pungens* Lam., *Pinus rigida* Mill. and *Pinus virginiana* Mill. Slopes are dominated by *Quercus coccinea* Muenchh. and *Q. montana* Willd., with *Acer rubrum* L., *Nyssa sylvatica* Marsh. and *Oxydendrum arboreum* L. in variable amounts. A thick layer of ericaceous shrubs including *Kalmia latifolia* L. and *Vaccinium* spp. is present throughout. Sheltered moist coves and slopes are dominated by large *Tsuga canadensis* (L.) Carr. in the overstorey and dense *Rhododendron maximum* L. in the shrub layer (see Newell & Peet 1998 for a detailed account of pre-fire vegetation). Evidence from fire scars and tree cores suggests that in the last 150 years Linville Gorge has been subject to several fires, varying in intensity and extent (C. Frost, unpublished data), with catastrophic crown fires in 1860 and 1915. Several low intensity surface fires also occurred, but their extent and frequency of occurrence are unknown. Prior to November 2000, when an unattended campfire ignited a wildfire that burned over 2000 ha within the wilderness boundaries, there had been no widespread surface fire since the 1950s.

DATA COLLECTION

A series of permanent plots was established and sampled in Linville Gorge in the summer of 1992 as part of a regional vegetation classification (Newell 1997; Newell & Peet 1998). Twenty-five of these plots were relocated and resampled during the summer of 2003. Five unburned plots were chosen to represent the major community types and served as controls for any major changes in vegetation that may have resulted from factors other than the fire. A preliminary analysis indicated that changes in mean species richness between 1992 and 2003 were not statistically significant at any scale in the unburned plots (M. Reilly, unpublished data). Thus, we concluded that the observed community dynamics in burned plots were attributable to fire effects and subsequent analyses were focused on the 20 burned plots.

All plots were set up following the Carolina Vegetation Survey protocol (Peet *et al.* 1998), with nomenclature following Kartesz (1994). Each of the plots consisted of a set of 10 × 10 m adjacent modules. Of the burned plots, 17 consisted of four modules (400 m²) and three consisted of two modules (200 m²). In each module two corners were sampled for the presence of all vascular plant species in a series of four nested quadrats increasing in size from 0.01 m² to 10 m². The rest of the 100-m² module was then searched for additional species. Post-fire canopy cover was estimated with a moosehorn densiometer in the four corners and centre of each module and put into one of the following cover classes: trace, 0–1%, 1–2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, and 95–100%.

All trees, shrubs and vines taller than 1.4 m were measured and assigned to diameter at breast height (d.b.h.) size classes (0–1 cm, 1–2.5 cm, 2.5–5 cm, 5–10 cm, 10–15 cm, ... 35–40 cm, > 40 cm). Trees > 40 cm d.b.h. were measured to the nearest centimetre. Post-fire tree sampling included measurement of both live and dead stems (standing and on the ground) to account for all stems found in 1992. These data were used to construct pre-fire basal area in 2000, providing a more accurate estimate of severity than using 1992 basal area because there had been considerable growth in some plots.

DATA ANALYSIS

Plots were classified into communities based on 1992 basal area using PC-ORD (McCune & Mefford 1999) following Newell & Peet (1998). Basal areas were relativized by plot totals to account for the three smaller plots in the data set. The flexible beta group linkage method ($\beta = -0.25$) and Bray–Curtis distance measure were used in the cluster analysis. The dendrogram was cut at 2.2848, resulting in four groups corresponding with the classification of Newell & Peet (1998). These groups were used as community classifications in subsequent analyses. A Kruskal–Wallace test was used to compare differences in reduction in basal area as data failed the equal variance test. Dunn's test was then used for multiple pairwise comparisons of reduction in basal area among community types. A one-way analysis of variance was used to test for differences in levels of canopy cover amongst the four community types. Tukey's test was then used for multiple pairwise comparisons of canopy cover among community types. All statistical analyses were carried out using SigmaStat 3.0 (SPSS Inc., Chicago, Illinois, USA).

Pre- and post-fire species-area curves were created for all plants together, for trees only and for herbs, shrubs and vines together, using non-linear curve fitting in SigmaPlot 2000 (SPSS Inc.). Herbs and vines could not be analysed separately because of their infrequent occurrence at scales $\leq 1 \text{ m}^2$ before the fire. They were combined with shrubs into a group (from here on referred to as non-trees) in which most species had the potential for long-distance dispersal via animal-dispersed fruits or light, wind-dispersed seeds. The mean numbers of species at each spatial scale (0.01 m^2 , 0.1 m^2 , 1.0 m^2 , 10 m^2 , 100 m^2 , 400 m^2) for each plot were fit to the power function to determine c - and z -values. Plots were also grouped and pre- and post-fire species-area curves were fit for each of the four community types using the number of species in each nested module within each plot.

We used paired t -tests to assess plot-level changes in c and z following fire, and linear regression to correlate changes in these parameters with fire severity. Fire severity was estimated as the percentage reduction in basal area after the fire. To assess how heterogeneity in light levels was related to the accumulation of species with area, the standard deviation of the 20 canopy cover

measurements from each plot was correlated with post-fire z -values using linear regression. All species present in a plot pre- and post-fire were separated into the number of survivors (species present pre- and post-fire), immigrants (species present only post-fire), and local extinctions (species present only pre-fire). We then used linear regression to investigate how the number of species that immigrated, survived and went extinct locally was correlated with fire severity. All analyses were performed for all plants together, trees only and non-trees.

Results

COMMUNITY COMPOSITION AND SEVERITY

Four community types were distinguished from the cluster analysis and were named following the classification of Newell & Peet (1998). Thermic pine forests ($n = 8$) were dominated by varying amounts of *Pinus pungens*, *P. rigida* and *P. virginia* in the overstorey. The midstorey was dominated by *Kalmia latifolia*, usually with the presence of some hardwood species, including *Quercus coccinea*, *Acer rubrum* and *Nyssa sylvatica*. Thermic oak forests ($n = 5$) consisted of varying amounts of *Q. coccinea*, *Q. montana* and *Q. alba* L., *Kalmia latifolia* was abundant in the midstorey along with *Acer rubrum*, *Pinus strobus* L. and *Oxydendrum arboreum*. Acidic slope forests ($n = 5$) were dominated by *Q. montana*, *A. rubrum* and *P. strobus*. The midstories were mixed, often with the presence of *K. latifolia*, *Rhododendron maximum* and *Tsuga canadensis*. Acidic cove forests ($n = 2$) were dominated by *T. canadensis* in the overstorey with a thick midstorey of *R. maximum*.

The mean and standard deviation of basal area reduction and canopy openness followed very similar patterns within communities (Fig. 1). Although both are good metrics of fire severity we chose to use basal

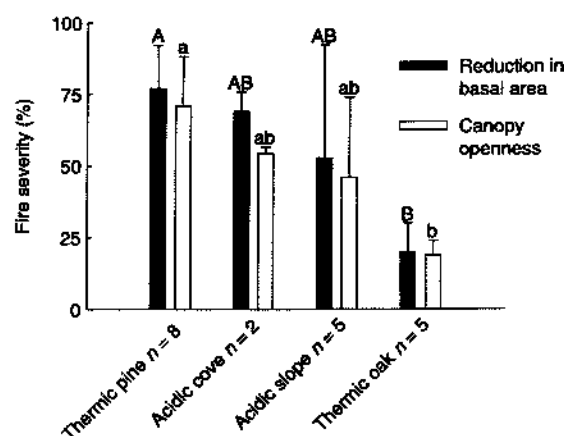


Fig. 1 Fire severity estimated as the mean percentage decrease in basal area, and the mean post-fire percentage canopy openness across four community types. Community means with the same letters are not significantly different at $P < 0.05$. Bars represent standard deviations.

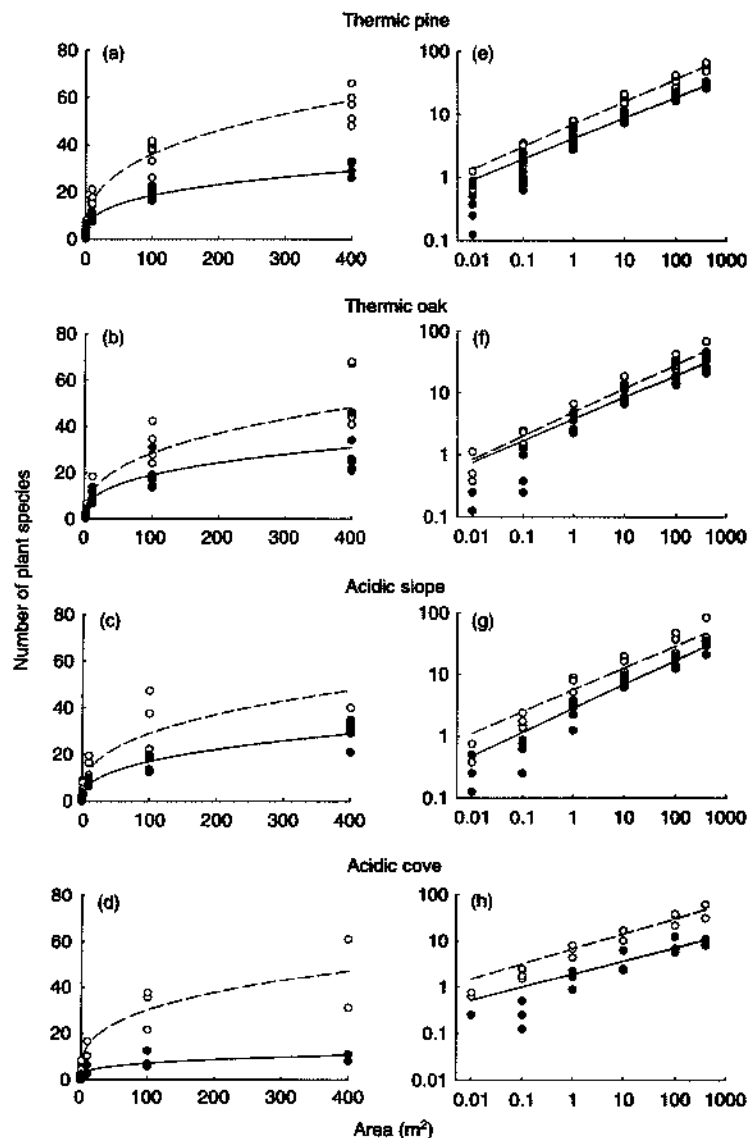


Fig. 2 Pre- and post-fire species-area curves displayed on arithmetic (a–d) and logarithmic (e–h) scales for all plants together in four community types. Pre-fire data are represented by closed circles and solid lines. Post-fire data are represented by open circles and dashed lines. Data points are the mean number of species at each spatial scale from each plot. Values of zero are not represented on the logarithmic plots.

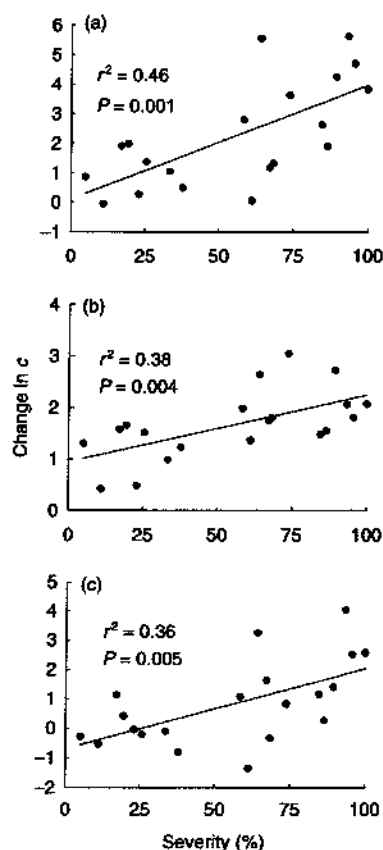
area reduction because it is based on a comparison of pre- and post-disturbance conditions and is representative of the decrease in overstorey dominance within a local community. Both basal area reduction and canopy openness were highest in thermic pine and acidic cove communities. These two community types showed relatively little variability in severity and canopy openness. Acidic slopes had the third highest mean reduction in basal area and levels of canopy openness but had a high degree of variability. Thermic oak plots had the lowest reduction in basal area and the lowest amount of canopy openness. Significant differences among community types were found for reduction of basal area ($P = 0.028$) and canopy openness ($P = 0.001$). Significant pairwise differences ($P < 0.05$) in reduction in basal area and canopy cover existed only between thermic pine and thermic oak forest types.

CHANGES IN THE SPECIES-AREA RELATIONSHIP FOR ALL PLANTS

Species-area curves for all plant species showed that absolute changes in species richness were positive and increased in magnitude with increasing scale (Fig. 2a–d). On a log-log scale, species area curves showed that, although absolute increases in species richness were greatest at large scales, proportional increases were approximately equal across all scales (Fig. 2e–h). Changes were greatest in acidic cove and thermic pine communities where severity was high, and smallest in the thermic oak communities where severity was generally low. Increases in species richness in acidic slope communities were intermediate in magnitude and exhibited a large amount of variability. Community-level pre- and post-fire comparisons of the fitted parameters c and z indicated that values of c increased after the fire but values of z changed very little (Table 1).

Table 1 Slope (z), coefficient (c) and correlation coefficients (r^2) values by community type for pre- and post-fire species-area curves for all plants

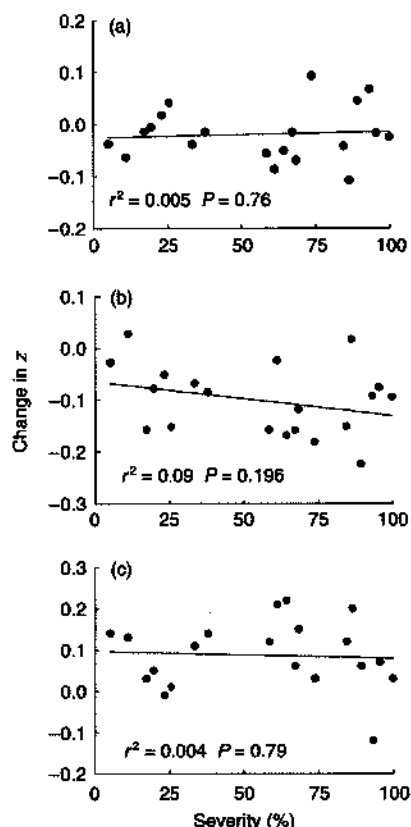
	Pre-fire			Post-fire		
	z	c	r^2	z	c	r^2
Thermic pine	0.32	4.12	0.97	0.36	7.06	0.97
Thermic oak	0.35	3.83	0.85	0.38	4.91	0.81
Acidic slope	0.39	2.73	0.92	0.36	5.78	0.76
Acidic cove	0.29	1.99	0.79	0.33	6.88	0.87

**Fig. 3** Linear regression results for the relationship between severity (% reduction in basal area) and change in c for (a) all plants together, (b) trees only, and (c) non-trees.

Pairwise t -tests between pre- and post-fire values of c and z for each plot showed statistically significant increases in c ($P < 0.0001$) but no significant change in z -values ($P = 0.11$). Changes in c were significantly and positively correlated with severity (Fig. 3a) whereas no significant relationship was found between changes in z and severity (Fig. 4a). There was no relationship between variability in canopy cover within a plot and post-fire z -values ($P = 0.59$, $r^2 = 0.016$).

CHANGES IN THE SPECIES-AREA RELATIONSHIP FOR TREES

Species-area curves for trees showed that absolute changes in species richness were positive at all scales

**Fig. 4** Linear regression results for the relationship between severity (% reduction in basal area) and change in z for (a) all plants together, (b) trees only, and (c) non-trees.

(Fig. 5a–d). Although absolute increases in species richness were highest at large scales, log-log scale species-area curves showed that proportional increases were highest at small scales and decreased in magnitude with increasing scale (Fig. 5e–h). Changes were again greatest where mean severity was high (acidic cove and thermic pine), smallest in thermic oak and intermediate and highly variable in acidic slope communities. Values of c increased but values of z decreased (Table 2).

Pairwise t -tests between pre- and post-fire values of c and z for each plot showed statistically significant increases in c ($P < 0.0001$) and statistically significant decreases in z -values ($P < 0.0001$). Changes in c were significantly and positively correlated with severity (Fig. 3b) whereas no significant relationship was found between changes in z and severity (Fig. 4b). There was no relationship between variability in canopy cover within a plot and post-fire z -values ($P = 0.44$, $r^2 = 0.03$).

CHANGES IN THE SPECIES-AREA RELATIONSHIP FOR NON-TREES

Species-area curves for non-trees showed that absolute changes in species richness differed across scales in magnitude as well as direction in some cases (Fig. 6a–d). Species richness actually decreased at scales $\leq 0.1 \text{ m}^2$ in

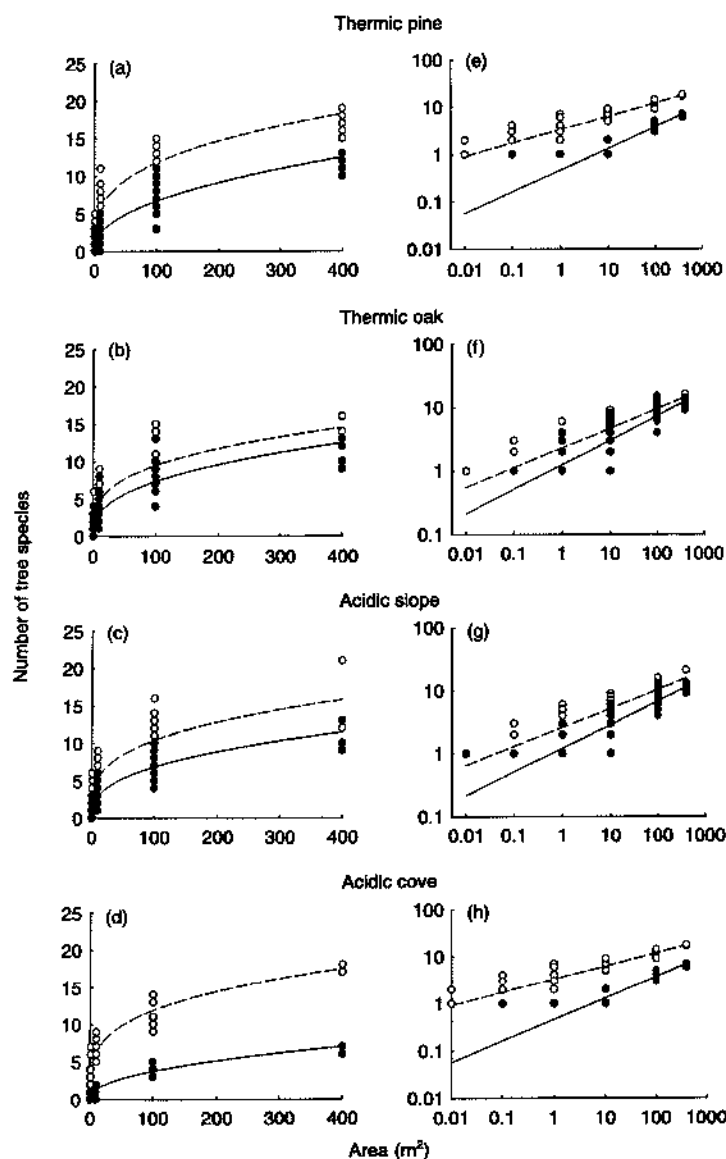


Fig. 5 Pre- and post-fire species-area curves displayed on arithmetic (a–d) and logarithmic (e–h) scales for trees in four community types. Pre-fire data are represented by closed circles and solid lines. Post-fire data are represented by open circles and dashed lines. Data points are the mean number of tree species at each spatial scale from each plot. Values of zero are not represented on the logarithmic plots.

Table 2 Slope (z), coefficient (c) and correlation coefficients (r^2) values by community type for pre- and post-fire species-area curves for trees

	Pre-fire			Post-fire		
	z	c	r^2	z	c	r^2
Thermic pine	0.45	0.85	0.89	0.32	2.75	0.91
Thermic oak	0.38	1.25	0.86	0.31	2.30	0.84
Acidic slope	0.37	1.21	0.87	0.30	2.61	0.85
Acidic cove	0.45	0.46	0.89	0.28	3.31	0.89

thermic pine and oak communities. Relative changes in species richness at scales $\geq 0.1 \text{ m}^2$ were positive in direction and increased in magnitude with spatial scale in thermic pine, thermic oak and acidic cove communities

(Fig. 6e–f,h) but were even across scales in acidic slope communities (Fig. 6g). Changes were particularly high in acidic cove communities where there was extremely low species richness pre-fire. Absolute changes were generally much lower in thermic oak and acidic slope communities. Values of c and z increased in all communities, although the change in z for acidic slopes was negligible (Table 3).

Pairwise t -tests between pre- and post-fire parameters of species-area curves per plots showed statistically significant increases in both c ($P = 0.017$) and z ($P = 0.0002$) after the fire. Changes in c were significantly and positively correlated with fire severity (Fig. 3c) but there was no significant relationship between severity and change in z (Fig. 4c). There was no significant relationship between post-fire z and the standard deviation of canopy cover per plot ($P = 0.30$, $r^2 = 0.06$).

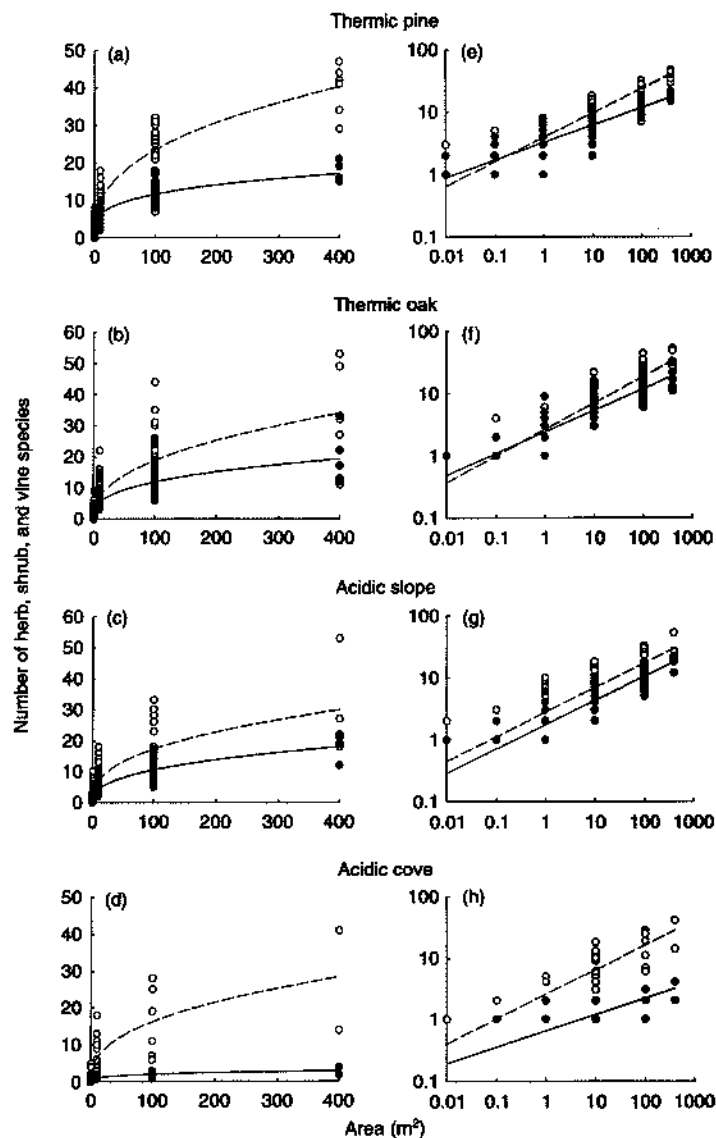


Fig. 6 Pre- and post-fire species-area curves displayed on arithmetic (a–d) and logarithmic (e–h) scales for non-trees in four community types. Pre-fire data are represented by closed circles and solid lines. Post-fire data are represented by open circles and dashed lines. Data points are the mean number of non-tree species at each spatial scale from each plot. Values of zero are not represented on the logarithmic plots.

Table 3 Slope (z), coefficient (c) and correlation coefficients (r^2) values by community type for pre- and post-fire species-area curves for non-trees

	Pre-fire			Post-fire		
	z	c	r^2	z	c	r^2
Thermic pine	0.28	3.24	0.86	0.39	3.90	0.90
Thermic oak	0.35	2.42	0.72	0.43	2.64	0.71
Acidic slope	0.39	1.74	0.82	0.40	2.77	0.70
Acidic cove	0.26	0.65	0.72	0.40	2.55	0.69

IMMIGRATION, SURVIVORSHIP AND LOCAL EXTINCTION

The number of local extinctions among all plants was low, with a mean and standard deviation of 7.0 ± 3.9

species per plot. Non-trees had a higher mean number of local species extinctions per plot (4.8 ± 2.9) than trees (2.3 ± 1.7 species). Mean survivorship of all plants was higher than extinction at 20.5 ± 6.8 species per plot and lower for trees (8.8 ± 2.4 vs. 11.7 ± 5.8 for non-trees). Mean immigration of all plants was much greater than the number of local extinctions or surviving species (35.6 ± 19.5) and was much lower for trees than non-trees (7.4 ± 3.4 vs. 28.3 ± 17.5). Results of linear regression indicated that for all plants immigration was positively and significantly related to severity ($P = 0.001$, $r^2 = 0.44$), whereas there was no relationship between severity and local extinction ($P = 0.95$, $r^2 = 0.016$) or survivorship ($P = 0.59$, $r^2 = 0.0003$) (Fig. 7a). Similar patterns to those for all species were seen for trees and non-trees ($P = 0.001$, $r^2 = 0.46$ and $P = 0.005$, $r^2 = 0.37$ for the relationship between severity

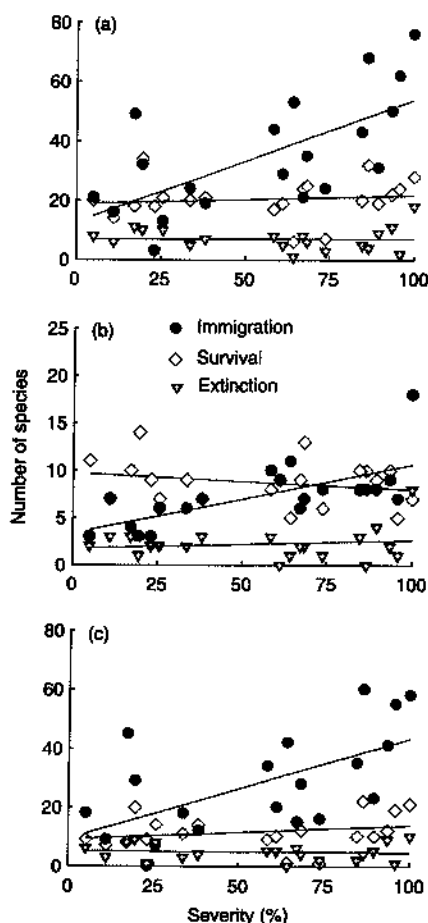


Fig. 7 Linear regression results for the relationships between severity (% reduction in basal area) and immigration, extinction and survivorship of species in local forest communities for (a) all plants together, (b) trees only, and (c) non-trees.

and immigration, $P = 0.51$, $r^2 = 0.02$ and $P = 0.77$, $r^2 = 0.005$ for extinctions and $P = 0.32$, $r^2 = 0.05$ and $P = 0.30$, $r^2 = 0.06$ for survival, Fig. 7b,c).

Changes in diversity at the plot level were driven predominantly by herbaceous species, which comprised 66% of all immigrants. Across the whole sample the total number of herbaceous species increased from 55 to 133. The family Asteraceae dominated forb immigration. The forb species with the highest rates of immigration were *Erechtites hieracifolia* L. Raf., *Eupatorium rugosum* Houttuyn., *Solidago altissima* L., *Lactuca canadensis* L., *Erigeron canadensis* L., and *Erigeron canadensis* var. *pusilla* (Nutt.) Ahles. Graminoid immigration was dominated by *Andropogon virginicus* L. and several species of the genus *Dicanthelium*. Fern immigration was dominated by *Dennstaedtia punctilobula* (Michx.) Moore. Tree species comprised 23% of all immigrants, with *Liriodendron tulipifera* L., *Paulownia tomentosa* (Thunberg) Steudel, *Betula lenta* L., *Robinia pseudoacacia* L., *Sassafras albidum* (Nutt.) Nees and *Ilex montana* (Michx.) Torrey accounting for more than half of the trees. The total number of tree species across the whole sample increased from 27 to 35. Shrubs and woody vines comprised 11% of all immigration. The

total number of shrub and vine species across the whole sample increased from 25 to 32. *Vitis aestivalis* Michaux, *Rubus argutus* Link, *Vaccinium corymbosum* L., *Rubus alleghaniensis* Porter and *Robinia hispida* L. together composed over half of all the immigration of shrub and vine species.

Most local extinctions involved infrequent species that occurred in only a few plots. The one frequent species with a notable rate of local extinction was *Pinus strobes*, which has been noted for its sensitivity to fire elsewhere (Blankenship & Arthur 1999). The only tree species lost from the entire sample, *Fagus grandifolia* Ehrhart and *Cornus florida* L., are also currently suffering declines in other parts of the region due to pathogens that may have exacerbated fire effects. The only shrub species that was lost from the whole sample was *Castanea dentata* (Marsh.) Borkh., whose pre-fire presence was presumably due to stump sprouts. There were several herbaceous species that went locally extinct after the fire, but only a few were lost from the entire sample. Those that were lost from the sample and occurred in more than three plots include *Arisaema triphyllum* (L.) Schott and *Maianthemum racemosum* (L.) Link.

Discussion

EFFECTS OF FIRE ON SPECIES-AREA CURVES OF ALL PLANTS

Changes in species richness of all plants are consistent across scales up to 400 m² after fire in the southern Appalachians. Despite considerable variation in severity and increases in absolute species richness ranging from just a few species to over 60 species, proportional changes were constant across five orders of magnitude, as indicated by the lack of changes in the slopes (z -values) of the species-area curves. Our results suggest that it is equally important to include both z and c when examining the species-area relationship (Rosenzweig 1995) and that although severity is important in predicting fire impacts on community diversity, these changes are generally independent of the scale of observation. Thus, fire in the southern Appalachians increases alpha diversity depending on severity, but has little effect on beta diversity and species accumulation rates at scales from 0.01 m² to 400 m².

The notion that spatial aggregation of conspecifics resulting from limited dispersal determines the rate of species turnover within local communities (Hubbell 1979; Condit *et al.* 2000) is supported by both theoretical models (He & Legendre 2002) and empirical data (Plotkin *et al.* 2000). The more clumped the distributions of species become, the steeper the slope of the species-area curve. As the degree of species mixing in space increases, the slope of the species-area curve decreases because most species will be found at smaller scales and few are added with more area. Though we did not map species distributions within plots, the lack of change in z supports the idea that the fire did not

alter the spatial pattern and degree of species mixing as a whole. Hughes & Fahey (1991) similarly found that disturbance from overstorey removal in a northern hardwood forest had little effect on the spatial pattern of understorey species, and that the location of predecessors before disturbance was a strong predictor of the spatial distribution of species after canopy removal. One possible explanation for a lack of changes in spatial distribution after disturbance lies in the patterns of survivorship, local extinction and immigration.

The low rates of extinction within plots indicated that most of those species present before the fire were also present afterwards as surviving stems or resprouts, thus maintaining the pre-fire spatial distribution of individual species. Community composition before the fire was largely comprised of woody species, many of which are fire adapted. In thermic oak and acidic slope communities, fire severity was mostly low to moderate. Several species that dominate these deciduous communities (*Quercus* spp., *Acer rubrum*, *Nyssa sylvatica*, *Kalmia latifolia*, *Vaccinium* spp.) can survive low severity fire by resprouting from underground root systems. Though fire severity and stem mortality in thermic pine forests was very high, post-fire dominance of yellow pine species (*Pinus pungens*, *P. rigida* and *P. virginiana*) was maintained by abundant seedling establishment from the canopy seed banks of either serotinous or persistent cones. In acidic cove forests where severity was high and pre-fire species richness was extremely low, the two dominant species, *Tsuga canadensis* and *Rhododendron maximum*, suffered very high mortality. However, both of these species were ubiquitous and evenly distributed within the acidic cove plots, and their loss had little effect on species turnover and the value of z .

Patterns of survivorship may account for the lack of change in z , but local recruitment of tree seedlings at small scales and immigration of non-trees at larger scales are responsible for the change in c and increases in species richness at all scales. Most studies of species-area curves have focused little attention on c . It has generally been interpreted as the number of species at the scale of one unit at which the study is being conducted (α diversity). Rosenzweig (1995) suggests that c is more than just a coefficient, but is important in determining the initial rate at which species accumulate at fine scales before reaching one unit of area (1 m² in this study). A second interpretation of c relates the parameter specifically to the density of individuals. Hubbell (2001) relates species-individual curves to species-area curves under the assumption that the relationship between area and individuals increases linearly and density is constant. Starting with the power function $S = cA^z$, c is replaced with p , where p = the density of individuals and $J = pA$, where J = the number of individuals. In this case the species-individual curve is predicted with the formula $S = J^z$. This formulation allows for a density-independent comparison of the accumulation of species.

The two interpretations of c are not mutually exclusive, and to some extent actually support each other.

If c increases because of higher richness at small scales, the effect can be attributed to an increase in density of individuals. Denslow (1995) suggested using the density hypothesis as a null model for looking at the effects of canopy gaps on diversity. Evidence that the density hypothesis explains increases in richness has been found in both temperate and tropical rain forest trees (Busing & White 1997; Hubbell *et al.* 1999), but additional analyses have shown that it generally only holds true for shade-tolerant species and not for intolerants (Busing & White 1997; Schnitzer & Carson 2001).

Though counting individuals is possible in studies of mature trees, accurate estimates of density were impossible in our study because of the large number of clonal species present in the herbaceous and shrub layer. Photographs taken pre- and post-fire at each plot attest that increases in density have occurred, especially in high severity plots, but an accurate quantitative estimate is not available. Our best estimate of changes in density can be made using presence of species at the smallest scale (0.01 m²). At such fine scales it has been suggested that richness is fundamentally constrained by density (Preston 1960; Fridley *et al.* 2005). Williams (1996) suggests that, at fine scales, mean species richness is actually a measure of the probability of finding an organism, and it may thus serve as a rough estimate of density. Using this approach, our data suggest that, on average, density within 0.01 m² plots has doubled from 0.24 species to 0.49 species and we cannot rule out the possibility that increases in richness are due to the increase in number of individuals.

EFFECTS OF FIRE ON SPECIES-AREA CURVES OF TREES

Changes in species richness of trees after fire in the southern Appalachians are not consistent across scales. Increases in post-fire values of c indicate increases in alpha diversity at small scales, but decreases in z -values indicate that increases in richness are smaller at larger scales and rates of species accumulation and beta diversity in local communities decrease after fire. With the exception of a few species (*Prunus pennsylvanica* L. f. and *Liriodendron tulipifera*), there is little evidence to suggest that many trees in the southern Appalachians have seeds that remain dormant in the soil for prolonged amounts of time (US Department of Agriculture 1974). Therefore, scale-dependent changes in species richness are likely to result from patterns of dispersal and immigration.

The removal of recruitment limitation by fire increases both densities of seedlings at small scales and the initial rate of species accumulation with area, supporting the interpretation of c by both Rosenzweig (1995) and Hubbell (2001). However, as most trees in the southern Appalachians are dispersal limited, with the majority of seeds of most species falling within 50 m of the parent tree (Clark *et al.* 1998), seedling recruitment is generally limited to those species present

in the local community that survived the fire. Immigration is limited to those species found within close proximity (≤ 50 m) of our plots and the few species in the landscape capable of long-distance dispersal by either wind (*Betula lenta*, *Salix* spp.) or birds (*Amelanchier arborea* Michaux f., *Ilex montana*, *Magnolia fraseri* Walter). Although local seedling recruitment after fire increases species richness at small scales, lack of immigration at larger scales decreases z , as most trees present in the canopy are now present at small scales in the seedling layer and few new species are encountered by increasing scale of observation.

EFFECTS OF FIRE ON SPECIES-AREA CURVES OF NON-TREES

Species-area curves for non-trees had higher c - and z -values post-fire and both absolute and proportional increases differed across scales. In addition to increased species richness at scales > 1 m², rates of species accumulation and beta diversity also increased in non-trees after the fire. The cumulative effects of similar directional changes in species richness across scales for non-trees and trees account for changes across scales in all plants. However, the contrasting changes in z -values between non-trees and trees result in the lack of change in z -values of all plants and are due to differences in the capacity for long-distance dispersal and contrasting patterns of immigration.

Changes in species-area curves for non-trees were driven predominantly by the immigration of light-seeded herbaceous species, capable of dispersing long distances by wind. Although several shrub and vine species in our sample are capable of being dispersed by birds over long distances (*Vaccinium* spp., *Vitis* spp., *Rhus* spp.), the available species pool within the landscape is limited compared with that of herbs. With the exception of a few herbaceous species common in plots of high fire severity, most immigrating non-tree species were represented by a single or a few individuals. This localized pattern of immigration within plots may create spatial variation in directional changes in small-scale density and species richness, corresponding with our observed changes in c . However, spatial segregation and lack of species mixing at small scales increases rates of species accumulation with area and beta diversity (z -values), resulting in large changes in species richness at the plot level.

EFFECTS OF FIRE ON PROCESSES OCCURRING AT DIFFERENT SCALES

At the smallest scales (≤ 1 m²), inferences about the effects of fire on processes determining species richness come from an interpretation of changes in c . Increases in c after the fire suggest an increase in density of potentially competing individuals. However, the effects of increased density on competition may be mitigated by the removal of large size differences that create com-

petitive asymmetries between growth forms (i.e. trees and herbs), and by increased levels of light resources. Much of the observed increase in species richness at small scales can be attributed to reduced competition and an increase in recruitment of species present before the fire. However, high rates of immigration suggest that dispersal-driven processes such as mass effects can also promote species coexistence even at small scales after disturbance. During post-fire succession it is likely that the role of competition will increase and the role of mass effects will decrease as dominance of woody species increases, canopies recover and light levels are reduced. Immigration will decrease and local extinction rates will increase as populations of shade-intolerant herbs thin, driving diversity back to pre-fire levels.

An interpretation of changes in the z -values from species-area curves provides a logical means to assess how habitat heterogeneity promotes species coexistence at intermediate scales (1–100 m²). A lack of either a change in z -values or significance in the correlation between variation in canopy cover and post-fire z -values suggest that fire has little effect on habitat heterogeneity and species turnover at these scales. Although we found significant decreases in z -values for trees and increases in z -values for non-trees, these changes result from contrasting patterns of immigration and dispersal, rather than variation in canopy cover or habitat heterogeneity. On the contrary, plots with the greatest changes in species richness were those where severity was uniformly high due to an increased role of mass effects at intermediate scales. Although others have suggested that wind disturbance may promote species coexistence by increasing spatial heterogeneity in both canopy cover (Denslow 1980) and local topography through the creation of pits and mounds (Battaglia *et al.* 1999), our data suggest that fire in the southern Appalachians does little to increase species richness through increased spatial heterogeneity at scales below 400 m². However, the creation of spatial heterogeneity after fire may be more apparent at larger scales where differences in severity across landscape gradients maintain heterogeneity.

At scales greater than 100 m² we are limited to interpreting changes at the plot level and across our entire sample. High rates of immigration post-fire are strong evidence that the role of mass effects has greatly increased, especially given the lack of change in species richness in the five unburned plots. Although recruitment of species from dormant seeds present in the soil is possible, only a few new species found in our plots are reported to be capable of long-term dormancy. Instead, most immigrants (58 of 93) in the 20 plots we measured post-fire were present elsewhere in the landscape within the 181 originally established plots (C. Newell, unpublished data). Assuming that these species were producing propagules pre-fire, their absence during the initial sampling was likely to be due to recruitment limitation created by closed canopies

and thick layers of organic matter, both of which were reduced by the fire. Despite the intensive sampling of 181 plots pre-fire, a precise estimate of species richness is difficult, and whether or not the 35 species present post-fire that were not present in the initial sampling were present in Linville Gorge is unknown. However, at some scale the fire in Linville Gorge did little to change species richness, and effects on species diversity were due only to a redistribution of the relative abundances of species.

Despite the increased influence of mass effects in determining species richness of all plants, the importance of mass effects differs among functional groups. The potential for mass effects to determine species richness depends on the number of dispersive species within the species pool of the surrounding landscape. As most tree species in the region are dispersal limited (Clark *et al.* 1998), mass effects influence tree species richness only slightly. In addition, it is likely that mass effects are only responsible for the presence of shade-intolerant species (*Liquidambar styraciflua*, *Prunus* spp., *Salix* spp. L.) that frequently immigrated post-fire, and that the role of mass effects for the more shade-tolerant species has not been altered. On the contrary, light-seeded, shade-intolerant herbaceous species are plentiful in the region, and mass effects resulted in large increases in non-tree species richness at larger scales. It appears that the role of mass effects in determining species richness therefore decreases as the potential for long-distance dispersal within a species pool decreases.

Conclusions

Fire alters the relative importance of ecological processes occurring at different scales in southern Appalachian forest communities. Although competition may be important in determining species richness at small scales in mature forest communities, our results indicate that the role of competition decreases after fire because light availability increases and competitive asymmetries between growth forms with large size differences are reduced. Once competition is reduced, the importance of mass effects increases at smaller scales and dispersive species in the landscape colonize disturbed areas at low levels of abundance. Our results do not support the hypothesis that increases in species richness are related to increased habitat heterogeneity at the local community level. At scales $\geq 100 \text{ m}^2$ the importance of mass effects is increased by the opening of the forest canopy, which allows for the coexistence of highly dispersive, light demanding species that can immigrate over large distances and those mature forest species that can survive fire. This increases species richness at all scales within local communities but does not affect the rate of species accumulation with area. For guilds of species, such as trees, that are generally dispersal limited, species richness increases at smaller scales, but mass effects are not important and species richness at large scales is limited by the number of spe-

cies present in the surrounding landscape. Likewise, increases in richness of non-tree species are less apparent at small scales because most of the immigrating species have low densities and occur infrequently at small scales. The effects of fire on species richness must be considered in terms of the severity of disturbance, the spatial grain of observation and the capacity for dispersal of the species present in the surrounding landscape.

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